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ABSTRACT

Preference reversals (PRs) occur when one's preferences over the same items change depending upon how one is asked to construct a preference. PRs are a robust phenomenon which lead to suboptimal real-world decision-making. Despite this, it remains unclear why PRs occur. This study investigated whether biological procedural invariance (i.e. different procedures are associated with different underlying mechanisms) could elucidate why PRs occur. Seventeen participants were scanned via *f*MRI whilst a) expressing preferences between two probabilistic wins or two probabilistic losses (one high and one low magnitude) and, b) reporting a monetary amount (valuation) according to how much they wanted to sell a potential winning gamble for or how much they would pay to forgo a potential loss. Participants' valuations closely followed expected value. Choice behaviour, however, was more prone to bias due to unequal weighting of either magnitude or probability. Preference formation during both valuation and choice was associated with fronto-parietal neural activity. Within this system, valuation was associated with greater activity in dorsolateral prefrontal cortex and caudal anterior cingulate cortex whilst choice was associated with greater activity in the insula, horizontal inferior parietal sulcus, posterior cingulate cortex and somatosensory cortex. The combination of behavioural and neuroimaging data may suggest that participants used a mathematical approach to formation of valuations but choices were subject to emotional influence. These findings may provide support for a biological procedural invariance view of gambling preference reversal. These findings are difficult to accommodate within explanations that rely on modifications to expected utility and prospect theory.

1. INTRODUCTION

Preference reversals occur when one's own preference for one particular item over another changes dependent upon how one is asked to provide the preference. For example, when providing a monetary valuation of two dinner sets in isolation, one containing 24 pieces in good condition (set L) and another containing 31 pieces in good condition and 9 pieces that are broken (set M), set L is typically ascribed a higher buying price. However, when both sets are shown in tandem and the individual is asked to choose between them, set M is typically preferred, thus indicating that preferences are unstable (Hsee, 1988). In the literature, the preference reversal (PR) phenomenon is observed when participants are presented with a pair of risky gambles matched for expected value, such that one gamble has a low payout and high win probability (referred to hereafter as the "P-bet"), whilst the other has a higher payout value but lower probability (referred to as the "$-bet"). Under these conditions participants typically choose the high probability P-bet when asked to make a straight forward choice; but when asked to ascribe a monetary value to each bet the high payout $-bet typically receives a greater valuation (Lichtenstein and Slovic, 1971; Lindman, 1971; Slovic & Lichtenstein, 1968). The phenomenon has proved to be extremely robust and has been observed consistently across various contexts and conditions (Lichtenstein & Slovic, 2006; Thaler, 1988) including in a study with actual gamblers in a Las Vegas casino (Lichtenstein & Slovic, 1973). However, despite the ease with which PRs can be elicited they have proven much harder to explain. Economists have frequently attempted to explain away the phenomenon as a form of artefact (Guala,

2000; Hausman, 1991) elicited by psychologists who “have the reputation for deceiving subjects” (Grether and Plot, 1979, p. 629). Gambling PRs are also of relevance to other aspects of everyday decision making. For example, PR-like phenomenon are often observed in health-related choices (Bleichrodt and Prades, 2009; Oliver, 2006) and policy decisions (Amiel et al., 2005) which can lead to sub-optimal choices involving distribution of one’s own income and attitude towards risky medical procedures dependent on how risk and reward is framed.

In relation to economic theory, PRs constitute a violation of at least one of the key axioms of expected utility theory which proposes that for any given series of alternatives, humans will consistently choose the option with the highest value (or “utility”) according to a fixed equation. Utility theory explicitly assumes that preferences are *independent* (i.e. that the value attributed to an option is unaffected by the presentation of other options) and show *procedural invariance* such that equivalent procedures for assessing preference should yield the same choices. A number of authors have argued that PRs might be explained via minor modifications to aspects of the independence principle (e.g. Loomes and Sugden, 1983; Fishburn, 1985; Holt, 1986; Karni and Safra, 1987; Segal, 1988), whilst other authors have argued that the effect represents a contradiction of procedural invariance (Goldstein and Einhorn, 1987; Tversky et al., 1990). In a seminal paper examining a number of possible interpretations for PRs in the context of the expected utility framework, Tversky et al. (1990) found that 90% of PRs elicited were attributable to procedural invariance rather than violations of other principles of expected utility (including the so-called intransitivity principle, see Kalenscher et al., 2010). The authors also concluded that PRs commonly occurred due to relative

overpricing of high value bets when a monetary value had to be ascribed to the bet. A plausible psychological explanation of this effect is that attention is more directed to the monetary amount associated with a bet when participants have to consider its value. This “scale compatibility” hypothesis offers a mechanism via which preferences are impacted by the procedure used to elicit the preference. Never the less, economic theorists continue to negate the role of procedural invariance and endeavour to specify models of preference formation which posit a unified mechanism underlying human choice in both valuation and forced choice contexts (e.g. Blavatskyy, 2009; Butler and Loomes, 2007; Loomes, 2010).

Functional brain imaging affords the opportunity to test whether these accounts of PRs are consistent with biological substrates underlying the valuation and forced choice procedures. Differences in brain activity between the two conditions would be consistent with a biological procedural invariance account in which the two modes activated segregated decision making system. The alternative is that the same areas are activated under both conditions, consistent with accounts which specify a single underlying mechanism for valuation and forced choice decisions. Previous neuroimaging studies have identified a system of brain regions involved in reward-related risky decision making involving the prefrontal, limbic and parietal regions. Within this system, there is a wealth of research that has elucidated the brain regions involved in stimulus valuation, notably the ventro-medial prefrontal cortex and ventral striatum (Cunningham et al., 2008; DeMartino et al., 2009; Elliott et al., 2008; Kable and Glimcher, 2009; Montague and Berns, 2002; Peters and Büchel., 2009), and action selection, particularly the lateral prefrontal cortex, parietal cortex and dorsal striatum (Balleine et al., 2007; Kable and Glimcher,

2009; Pesaran et al., 2008). Previous neuroimaging studies have also studied related framing effects in decision making. A reliably documented framing effect is an individual's tendency to be risk-averse when indicating preferences between risky outcomes that are framed as potential gains but risk-seeking when the risks are framed as potential losses, despite values and probabilities in both frames being equal (Kahneman and Tversky, 1979). De Martino et al. (2006) found that the amygdala was associated with choices to make decisions in accordance with the valence of the frame (risk-averse with rewards and risk-seeking with losses) compared to choices which ran counter to the frame, thus providing evidence for a mediating effect of emotion on this decision bias, a finding strengthened by other researchers investigating framing effects in risky situations (Roiser et al., 2009; Zheng et al., 2010) and social evaluations (Deppe et al., 2005). These findings naturally lead to the hypothesis that similar differences in emotional input during valuation and/or choice may account for the difference in behaviour between the two preference elicitation frames underlying PRs and that these should be reflected in the distribution of brain activity.

The objective of this study was therefore to investigate whether brain activity as measured by Functional Magnetic Resonance Imaging (*f*MRI), differed during preference formation under the two frames of the classic PR experiment. The first hypothesis states that the two task types will recruit different brain systems and that activation of these systems within the two task types leads to the recruitment of separable cognitive processes and, therefore, PRs occur due to the different output of two separable systems. The second hypothesis states that the brain systems involved in each task type will be overlapping. In this case, PRs potentially

occur due to differential functioning of discrete parts of the same system between each elicitation procedure.

2. METHODS

2.1. Participants

Seventeen right-handed participants took part in the study (*M* = 21.47 years, *SD* = 3.53, *Range* = 18-29 years). Participants were recruited from student populations at the University of Bath and University of Exeter. There were fourteen females and three males. All participants were volunteers who were taking part as they were interested in the research or having experience of *f*MRI or being part of a research study.

2.2. Experimental Tasks

Participants completed four tasks in the scanner; a Reward Valuation Task (Val-Rew), a Loss Valuation Task (Val-Loss), a Forced Choice reward task (Choice-Rew) and a Forced Choice Loss task (Choice-Loss). The order of the tasks for each participant was decided randomly by a random number generator (www.random.org). All rewards and losses were hypothetical. All tasks were back-projected onto a translucent screen located at the foot of the scanner bed, viewed through mirror mounted on the scanner head coil above the participant's eye-line.

2.2.1. Reward and loss valuation tasks

Each trial presented a single, hypothetical gamble stating an amount of money to be won or lost according to a probability. Reward magnitude was either High

(£200) (i.e. the "$-bet") or Low (£100) (the "P-bet"). These magnitudes were selected so that they would appear to be attainable and realistic potential wins/losses whilst the difference between them was large enough to be salient to our sample. Probabilities ranged from 0.1 to 1.0 in 0.1 intervals. A full list of gambles used in the tasks is included in Table 1.

Participants were instructed to create a valuation of discrete gambles. In the *Val-Rew* task participants were instructed to report a monetary amount corresponding to how much they would sell the gamble for. The instructions for the *Val-Rew* are shown below.

In this task, you will see some uncertain gambles. Each gamble consists in an amount of money that could be *won* with a certain probability. E.g. 50% chance of winning £20.

We just want you to watch each gamble and, while it is displayed, evaluate for yourself how much money you would want to sell the gamble for (i.e. its price). There are no right or wrong answers, just how much you think the gamble is worth. It could be a large or small amount, so you should feel free to choose a price between £1 and £200. After each gamble is presented, you will be able to indicate your preferred price using a sliding scale.

Sometimes you will see displays in which the numbers of the gamble have been replaced by letters so that the gambles have no meaning; these are just control displays which help us to analyse the responses to the real gambles. Please watch the screen as normal during these displays and then provide a fixed price of £200.

In the *Val-Loss* task participants were instructed to report a monetary amount corresponding to how much they would pay to ensure that the gamble (a potential loss) would not be played. Full instructions for the *Val-Loss* are shown below.

In this task, you will see some uncertain gambles. Each gamble consists in an amount of money that could be *lost* with a certain probability. E.g. 50% chance of losing £20.

We just want you to watch each gamble and, while it is displayed, evaluate for yourself how much money you would pay to make sure that the gamble didn't happen to you (i.e. its price). There are no right or wrong answers, just how much you think the gamble is worth. It could be a large or small amount, so you should feel free to choose a price between £1 and £200. After each gamble is presented, you will be able to indicate your preferred price using a sliding scale.

Sometimes you will see displays in which the numbers of the gamble have been replaced by letters so that the gambles have no meaning; these are just control displays which help us to analyse the responses to the real gambles. Please watch the screen as normal during these displays and then provide a fixed price of £200

A schematic of a valuation task trial is shown in Figure 1. After the gamble was shown, participants then reported their valuation on a measure similar to a visual analogue scale (VAS). At the apex of each line was a monetary amount (£1 on the left apex and £200 on the right apex). Participants moved a vertical bar left or right along the line to a region corresponding to their predetermined monetary valuation using left/right buttons on a two-button box. There were 20 possible positions in which the bar could be placed (i.e. moving in £10 intervals). The screen containing the gamble was presented for 5 seconds and the VAS presented for 7.5 seconds. An inter-trial interval (ITI) followed this consisting of a blank screen with a jittered duration between 3-12 seconds decided pseudo-randomly when the task was constructed.

Control trials were presented in which the numbers associated with the gamble were replaced by letters (e.g. '£XXX') so that no valuation could take place. During the rating of the control trials, participants were instructed to move the bar to £200

in every trial so that a motor movement was still performed. There were 12 control and 18 valuation trials in the Val-Rew with each gamble being presented once (apart from £200 at 50% chance which was presented twice). The task took nine minutes 54 seconds to complete excluding the time taken reading the instructions. There were 12 control trials and 13 valuation trials in the Val-Loss (for details of which gambles were presented see Table 1). The task took eight minutes 20 seconds to complete excluding the time taken reading the instructions. The Val-Loss was shorter so as to accommodate the scanning within a time period comfortable for the participant.

2.2.2. Reward and Loss Forced-choice tasks

The two forced-choice tasks presented gambles from the valuation tasks in two-alternative, forced-choice, scenarios. The Choice-Rew and Choice-Loss consecutively presented two potentially winning or two potentially losing gambles respectively. The instructions are shown below.

You will be presented with a series of choices involving two gambles.

Select which gamble you prefer.

There is no right or wrong answer. Just choose whichever you prefer.

Use the blue button to choose the amount in the left of the screen and the yellow button to select the amount on the right

After you have chosen, there may be a delay in which the choice remains on the screen. If this occurs do not make another response, just wait for the next choice.

Sometimes, the numbers in the choice will be replaced by letters, making it meaningless. In these cases, simply choose the gamble that is underlined.

A visual depiction of the task can be seen in Figure 2. During choice trials, a screen was presented for 5 seconds containing two gambles presented in pairs with one on the left and one on the right of the screen. The location of the gambles was counterbalanced and decided pseudo-randomly when the task was constructed. One of the alternatives had a reward of £100 and the other, £200. The probability of each alternative varied on each trial such that there were trials where the £100 gamble had the highest expected value compared to the £200 gamble and vice-versa (see Table 2 for details of how the gambles were ordered). Participants indicated which one of the two alternatives they preferred by way of a left/right button press on a two-button box. The control stimuli were the same as in the valuation tasks but presented in pairs and the participant was instructed to choose either the leftmost or rightmost gamble. Participants had to make an equal number of leftmost and rightmost selections in control trials. There were 18 choice trials and 12 control trials.

Following the choice screen, an ITI consisting of a blank screen with a centralised fixation point was shown for a jittered period of time (3-12 seconds) decided pseudo-randomly when the task was constructed. Following this, the next trial was presented. Each task took seven minutes and 36 seconds to complete excluding the time taken reading the instructions.

2.3. Data Analysis

2.3.1. fMRI acquisition and preprocessing

Blood oxygen-level dependent (BOLD) analysis was performed using a gradient-echo T2* weighted sequence (Echo Planar Imaging) through a 1.5 Tesla Phillips Gyroscan Intera located at the Peninsula Magnetic Resonance Research Centre at the University of Exeter, U.K. A 30^{o} tilted acquisition sequence was used in order to reduce signal dropout within the orbitofrontal lobes. The image parameters were as follows: TE 45ms; TR 3s; 38 slices; slice thickness 3mm; inter-slice gap 0mm; voxel size $3mm^{3}$; inter-scan interval 3s. The volumes present in the Val-Rew, Val-Loss, Choice-Rew and Choice-Loss were 200, 170, 155 and 155 volumes respectively. Images were analysed using SPM5 (Wellcome Department of Imaging Neuroscience, London, www.fil.ion.ucl.ac.uk/spm). Pre-processing consisted of slice time correction, motion correction, coregistration of each individual participant's mean resliced image to their T1-weighted structural image, segmentation, normalisation to the mean coregistered image and smoothing of the functional data using a FWHM 8mm kernel. A high-pass filter was applied to all images (128s) and autocorrelation of the hemodynamic response function was modelled as an *AR*(1) process. In the first level, movement parameters were entered as a regressor of no interest.

2.3.2 fMRI analysis

The fMRI statistical model assessed activations during the decision periods in the valuation or choice tasks corresponding to the period between the onset and offset of the presentation of the gamble or gamble pair (including control trials), modelled as discrete events with five seconds duration.

In the first level of analysis, statistical contrasts were created which compared the BOLD response to experimental events to their respective control events. In the valuation tasks this corresponded to the contrast *gamble minus control trial*, henceforth known as the “valuation period” activity and in the forced-choice tasks this corresponded to the *choice minus control trial* contrast, henceforth known as the “choice period”. Random effects analyses were performed by pooling these contrast images for each subject in a second level group analysis to assess consistent patterns of activity across participants.

The main objective of the study was to contrast activity during processing of valuations vs. making a forced choice. Thus, at the second level the output from the first level contrast from each task, i.e. valuation period and choice period, were directly contrasted. This produced two main contrasts for each reward type (valuation-choice under potential gain and valuation-choice for potential losses). Secondary to the main objective, we were interested in investigating whether the neural substrates related to the processing of valuation and choice separately was different when faced with rewards vs. losses. To explore overall effects of rewards vs. losses activity from both tasks involving rewards (valuation and choice) was compared to that within both tasks involving losses in factorial design. To investigate whether there were any differences within each task type, repeated

measures t-tests were used to compare BOLD signal derived from the first-level analyses within the reward valuation and, separately, within the choice tasks.

All co-ordinates shown are in Talairach space (Talairach and Tournoux, 1988) transformed from MNI space using Talairach Daemon (www.talairach.org) utilising a nearest gray matter search. This transformation method is in wide use within cognitive neuroscience research. For the reason that we did not specify any hypotheses concerning the loci of differential brain function, a cluster-wise analysis approach was taken whereby all voxels met a threshold of $p < .001$ (uncorrected) and met a cluster threshold of $p < .05$ (uncorrected).

3. **RESULTS**

3.1. Behavioural data

The mean valuations given by the participants in the Val-Rew and Val-Loss are shown in Figure 3. These graphs indicate that participant's valuations were generally close to expected value.

The number of all categories of participants combined choices and valuations of gambles are also shown in Figure 3. Previous work has shown that "standard" PRs where the P-bet is chosen over the $-bet but the $-bet receives a greater valuation, are more common than "non-standard" preference reversals, where the $-bet is chosen over the P-bet but the P-bet receives a greater valuation. Our results confirmed this finding with a significantly greater number of standard relative non-standard PRs, $\chi^2 = 77.87$, $p < .001$. Out of 222 choices for the P-bet 52.3% constituted PRs relative to the valuation condition (Lichtenstein and Slovic, 1971, 1973) whilst only 22.4% of the 67 choices recorded for $-bets were PRs.

In the loss valuation (loss-val) condition participants had to indicate an amount they would be prepared to pay to forgo the potential loss whilst in the Choice-Loss condition they had to indicate the gamble they would prefer to pay i.e. the gamble which to them represented the lesser of the two losses. Thus standard PRs in this case would be choices for the low probability $-bet in the context of a higher valuation being attributed to the $-bet. Consistent with this, such a pattern was observed much more frequently than the occurrence of choices for P-bet which

were attributed higher values than the accompanying $-bet. The frequency of instances of PRs (37% of all trials) was much greater than instances of non-standard PRs (6.5%), $\chi^2 = 184.18$, $p < .0001$ (Figure 3).

In summary the behavioural data replicates the original gambling PR phenomena as well as demonstrating reliable PRs for gambles representing uncertain losses.

3.2. FMRI Results

3.2.1. Overlapping activity during the choice and valuation tasks

A conjunction analysis assessed regions which activated consistently across all conditions by combining 1 sample t-tests for each task (Val-Rew, Val-Loss, Choice-Rew and Choice-Loss). This showed overlapping activity within brain regions including bilateral dorsolateral prefrontal cortex (dlPFC) and dorsomedial frontal cortex, anterior mid-cingulate cortex (aMCC), bilateral inferior parietal cortex (iPC, BA40), bilateral precuneus, angular cortex and premotor cortex; Figure 4 shows the extent of overlapping regions within cortical areas from each task.

3.2.2. Difference in brain activity during the choice and valuation tasks

Direct statistical contrasts (repeated measures t-tests) between the two valuation (Val-Rew and Val-Loss) and two choice condition (Choice-Rew and Choice-Loss) were also carried out. This showed that some brain regions were more active in one task type versus the other (Figure 5). More specifically, the valuation minus

choice contrast yielded significant clusters within the left dlPFC (BA46), left supplementary motor area and the posterior midcingulate cortex (BA32). The choice minus valuation contrast yielded a greater number of significant clusters compared to the reverse contrast including a large cluster (349 voxels) within the left posterior insula in addition to the bilateral iPC (BA40), posterior cingulate cortex (PCC) and a region of the posterior midcingulate cortex that was caudal to the region from the earlier contrast (BA24). Other regions included the bilateral superior temporal cortex, supramarginal cortex, primary motor and somatosensory cortex.

Following from the main contrasts described above, the valuation and choice tasks were further split by gamble type (Reward / loss) to yield the following t-contrast images: Val-Rew vs. Choice-Rew and Val-Loss vs. Choice-Loss. The [(Val-Rew)-(Choice-Rew)] contrast yielded significant clusters of activity within the left dlPFC, medial frontal cortex (BA6), aMCC and bilateral supplementary motor cortex. The [(Choice-Rew)-(Val-Rew)] contrast produced significant clusters within the right iPC, medial frontal cortex (BA6), somatosensory cortex and posterior cingulate cortex. The [(Val-Loss)-(Choice-Loss)] contrast yielded only one significant cluster within the dlPFC while the reverse contrast, [(Choice-Loss)-(Val-Loss)], yielded significant clusters within the right iPC, left premotor and somatosensory cortex and the bilateral (predominantly left) insula.

To investigate potential differences in brain activity associated with reward type, each task type was compared across reward conditions to give the following contrasts; Val-Rew vs. Val-Loss and Choice-Rew vs. Choice-Loss. None of the

four contrasts produced any significant voxels. Furthermore, the overall effect of reward type was investigated by the following contrast, [(Val-Rew+Choice-Rew) vs. (Val-Loss+Choice-Loss)]. There were no significant clusters showing heightened activity in either reward type.

3.2.3 Parametric Analyses

In addition to the contrasts by task and gamble type described above we also assessed evidence for activity dependent upon the value of the difference in expected gamble in the choice tasks as well as the expected value of the chosen value in the choice task and the participants valuation and expected value of the gambles in the valuation task. None of these parametric analyses revealed any significantly activated voxels at the random effects level using the same statistical threshold used in the condition / task comparison analysis described above.

4. **DISCUSSION**

Preference reversals (PRs) are a well known phenomenon in human decision-making which have been the subject of extensive discussion by economists, psychologists and philosophers (Guala, 2000; Hausman, 1991; Grether and Plot, 1979), due to the fact that they appear to constitute a violation of expected utility theory. Key to this debate is whether PRs reflect a violation of procedural invariance or can be explained by the application of a single preference formation mechanism across contexts. The present study integrated data derived from neurobiological and behavioural performance in order to explore differences in neural processing underlying preference formation during valuation and forced choice preference elicitation condition. Contrasting BOLD responses while participants made either a forced choice between gambles or attributed a monetary valuation to a gamble revealed an overlap between brain areas recruited by the two tasks. However, there were also large differences in the extent and location of brain activity observed under valuation and forced choice conditions. The difference in brain activations between the two tasks potentially points towards biological procedural invariance between the two frames, a hypothesis that will be discussed shortly.

Consistent with previous findings standard PRs, where the P-bet is chosen over the $-bet for gains but the $-bet is given a higher value were significantly more common than the reverse pattern of preferences (Lichtenstein and Slovic, 1971, 1973; Lindman, 1971; MacDonald et al, 1992). In contrast, for losses choice of a gamble which a previously received the higher valuation in the valuation task

constitutes a PR and the classic PR phenomenon would be expected to be manifest as a choice for the high value / low probability £-bet alongside a lower valuation attributed to the P-bet. Consistent with this, choice of the £-bet combined with a higher valuation for the £-bet pattern was observed significantly more commonly than the opposite direction of PR in the present study. Under Loss conditions there was also a trend for more standard PRs to occur as the difference in expected utility (δEV) became positive (δEV was calculated as EV of $-bet – EV of P-bet, see Table 2). This behavioural trend violates assumptions put forward by expected utility theory, but does follow assumptions underlying prospect theory (Kahneman and Tversky, 1979) which states that humans are typically more risk-seeking in a loss domain so as to try to evade the negative emotional arousal experienced following a loss (Tom et al. 2007).

The *f*MRI findings indicated that both preference procedures were associated with an overlapping system of brain areas which included regions previously linked with value construction (Kim et al., 2009; McCoy & Platt, 2005[1]; Rangel et al., 2008). The dlPFC and iPC have been reliably implicated in working memory and computational processing (Miller & Cohen, 2001; Dehaene, 2009), whilst both the dlPFC and aMCC are known to exert a modulatory role on the brains reward system, influencing activity in downstream regions within the basal ganglia (Haber & Knutson, 2009). In particular, dlPFC has been implicated in maintaining representations of outcomes in working memory (Miller & Cohen, 2011) whereas the aMCC has been reliably implicated in conflict monitoring (Botvinick et al., 2004; Botvinick, 2007). Activity in the dLPFC and aMCC may work together in a complementary manner in order to process and compare valuations of items held

within working memory in order to select the optimal outcome (Haber & Knutson, 2009). In a review by Seitz et al. (2009), the medial frontal cortex was posited to process the valuation of items in an self-referential framework in line with findings suggesting that this region indexes the subjective mental concept of one's own self (Passingham et al., 2010) and may thus reflect ego-centric valuation of the gambles. The posterior cingulate cortex is involved in risk-processing and its potential role during valuation will be returned to in greater detail. The premotor cortex has been found to be sensitive to relative values of items when a motor response is required to obtain an outcome (Cisek & Kalaska, 2005; Pastor-Bernier & Cisek, 2011) and that activity within the premotor cortex preceding a planned motor response correlates with the salience of a potential reward, i.e. that motor movements towards aversive outcomes are suppressed (Bianchin & Angrilli, 2011), likely reflecting the end-product of the processing of the reward system. The angular gyrus has been traditionally associated with comprehension and production of language (Price, 2010) although it has also been associated with exact, rather than approximate, mathematical calculation (Jost et al., 2011; Stanescu-Cosson et al., 2000). Activity in this study may reflect such computational processing given that all gambles were well-defined thus exact calculation of a value was possible. Additionally, the angular cortex has been linked to a neural system involved in experience of regret associated with efforts to avoid aversive outcomes (Chandrasekhar et al., 2008) and activity within this region may reflect negative feelings associated with perceived experience of loss during valuation of both potential gains and potential losses.

When contrasting the two elicitation procedures it was found that there were differences in the magnitude of BOLD response in particular regions within this network with the valuation conditions being associated with greater activity in lateral and dorso-medial frontal regions and forced choice being associated with increased activity within lateral and medial posterior regions and the insula. The specific regions activated also offer clues as to the different cognitive and decision making processes recruited under the forced choice and valuation conditions and may offer support for procedural invariance accounts of PRs when combined with the findings of the behavioural data. Behavioural data indicated that participants' valuations followed very closely those calculated by expected utility theory. In contrast, participants did not express such "rational" behaviour in the forced choice task as evidenced by the frequency of PRs. This finding integrates well with the neurobiological results. Valuation was associated with increased activity in regions reliably implicated in "rational", cognitive, processing, namely the lateral prefrontal cortex and caudal anterior cingulate cortex (Miller and Cohen, 2001; Vogt et al., 2003). In contrast, *f*MRI findings suggest that the forced choice was associated with activity in neural regions that have been robustly associated with emotion processing, i.e. posterior cingulate and insula. Neurophysiological studies in monkeys performing eye-movement decision-making studies have found that the posterior cingulate cortex is responsive to both reward magnitude and probability and appears to have an evaluative role in determining whether rewards experienced following a particular action match expectations (McCoy & Platt, 2005[1]). In humans, the posterior cingulate cortex has also been implicated in modulating individual attitudes towards risk (Engelmann and Tamir, 2009; Watson, 2008). The insula has a well-documented role in processing experience of negative

emotions (Calder et al., 2001; Sanfey et al., 2003) and has been implicated in decision-making, specifically the precise coding of risk probabilities (Clark et al., 2008; Quartz, 2009). It has been suggested that the insula encodes the level of aversion associated with experience of risky outcomes (Mohr et al, 2010) which would concur with our findings that insula activity was more prevalent in the loss domain as these choices would involve more negative emotion (Kahneman & Tversky, 1979).

Other work has suggested the existence of interactions between the posterior cingulate and insula underlying the integration of emotional states in decision-making (Quartz, 2009). In a recent paper, neural signatures of transitivity (another violation of expected utility theory) were explored by presenting participants with forced choices between two gambles with varying magnitudes and well-defined risks. Interestingly, the interplay in the interaction between posterior cingulate cortex and insula was critical in coding subjective, context-dependent and local value of each choice (Kalenscher et al., 2010). The authors posited that the posterior cingulate cortex indexed an individual's response to risk while the insula indexed the urge to seek high rewards in line with findings indicating that insula activity correlates with excitement associated with high rewards during gambling (Li et al., 2009) i.e. low aversion to the risky outcome.

Although the finding of conjoint increased posterior cingulate and insula activity in the choice vs. valuation tasks may suggest heightened influence of emotion within the choice task, it is important to note that these regions have also been associated with other roles. The insula has commonly been associated with

emotional processing, but also with gustation, olfaction, processing of pain, switching, inhibition and response conflict (Chang et al., 2012; Menon and Uddin, 2012). The posterior cingulate cortex, in addition to being involved in emotion and reward processing, also has a role in sensory processing (Vogt et al., 1992; Vogt et al., 2003). Furthermore, it is perhaps not surprising that the two tasks are associated with somewhat different patterns of activation given that in one task the participant must map their valuations to a scale while in the other a choice must be formed. This study did not seek to suggest otherwise. Instead, it aimed to explore what were the processes underlying preference formation in the two tasks and how they differed, thus attempting to elucidate why PRs occur at all. To the best of our knowledge, this is the first neuroimaging study directly comparing the two tasks commonly used in the economic and psychological literature investigating PRs. The use of *f*MRI permitted the investigation of processes underlying the two tasks, thus providing ideas as to the potential reasons why PRs occur. Although other processes may be at play, the "rational vs. emotional" argument is strengthened by our behavioural findings, which showed that valuations very closely followed those calculated by expected value in contrast to the forced choice task where PRs (non-rational behaviour) were common. This study can be seen as a foundation from which to build future studies as targets for future research have been identified. Future work may wish to further explore the role of the posterior cingulate cortex and insula in decision-making and valuation with particular attention on how the interaction between these regions may lead to biases in choice behaviour.

Other brain regions also showing increased activity for the forced choice relative to the valuation procedure included the supplementary motor area, caudal anterior

cingulate cortex (both involved in response selection) and the iPC. The difference in BOLD response measured within the iPC was predominantly localised to the horizontal inferior parietal sulcus (HIPS), which has repeatedly been associated with arithmetical processing (Dehaene et al. 1998; Dehaene et al. 2004; Dehaene, 2009; Riviera et al. 2005) as well as being associated with reward processing (Liu et al., 2011). One explanation for enhanced activity in this region would be that there was an increased mathematical processing in the choice tasks over the valuation tasks as there are two gambles to process instead of one. However, this infers that the worth of the gambles in the choice frame was calculated mathematically. As has been concluded by our behavioural and *f*MRI results, the gambles during the choice frame were not treated in such an arithmetical manner. Alternatively parietal regions may be recruited by processing of ambiguous rewards. The iPC has been reliably associated with the processing of risky rewards (Bach et al., 2009; Vickery and Jiang, 2009) and has a role in representing the probability and / or reward magnitude of risky gambles (McCoy and Platt, 2005; Platt and Glimcher, 1999).

Within each type of elicitation procedure there was no significant difference in activity between gain and loss tasks suggesting that within each elicitation procedure the same processes occurred for constructing preferences between rewards and losses. This concurs with other literature showing that valuation of gains and losses are processed by similar neural regions (Breiter et al., 2001; Fitzgerald et al., 2009).

Our *f*MRI findings, supported by our behavioural findings, can be used to suggest that valuation is associated with dominance in “rational”, cognitive processing while forced choice is subject to contextual, affective, influence. This conclusion would therefore support Tversky et al.’s (1990) conclusion that procedural invariance is the driving force behind PRs, specifically the framing of the elicitation method is associated with formation of preferences using either a predominantly cognitive or emotional framework as evidenced by differential neural activity between elicitation methods. This has potential implications for usage of the evaluation and choice tasks in psychology and economic research in addition to real-world choices. Negative emotions such as anxiety, depression, disgust and fear have been found to significantly impact upon decision-making involving risks (de Visser et al., 2010; Heilman et al., 2010; Miu et al., 2008; Smoski et al., 2008). Our results could suggest that the frame of the preference elicitation method is important in motivating discrete types of preference formation strategies. Therefore, with situations associated with heightened emotion, for example, health-related decisions, it may be better to frame the scenario in such a way as to elicit a cognitive, analytical, framework. It would be of interest to investigate whether training individuals to manage emotion or be mindful of negative emotions during risk-related decision making would lead to a decrease in incidences of PRs.

One potential limitation was the absence of a transaction phase which has become common in economic and neuroeconomic literature using paradigms in which participants ascribing monetary amounts according to their willingness-to-pay (WTP) or willingness-to-sell (WTS) an item (DeMartino et al., 2009; Kahneman et al., 1990). During the transaction period the participant is offered a sum of money

(often randomly generated) and dependent on their WTP/WTS values, are given the money or keep the item. Such phases are designed with the aim of motivating the participant to provide their true WTP/WTP values. In our tasks, a transaction phase was not included in order to maximise the number of events measured within the scanner and allow time for investigation of preference of both gains and losses. We cannot say for certain whether the inclusion of a transaction phase would have elicited different preferences although future experiments may require the inclusion of a transaction phase.

We have elucidated differences, and similarities, between the neural and cognitive processes underlying preference formation in evaluative and forced choice frames. This work could potentially have effects on such domains as business, banking, marketing, healthcare or other such industry in which choice between uncertain options play an important role. Care needs to be taken to frame problem information situations such that consumers/decision-makers approach the formation of their preferences either in a rational, “cold”, framework or an emotional, “hot”, framework.

REFERENCES

Amiel, Y., Cowell, F., Davidovitz, L. and Polovin, A. (2007). Preference reversals and the analysis of income distributions. *Social and Choice Welfare*, 30, 305-330.

Bach, D.R., Seymour, B. and Dolan, R.J. (2009). Neural activity associated with the passive prediction of ambiguity and risk for aversive events. *Journal or Neuroscience*, 29, 1648-1656.

Balleine, B.W., Delgado, M.R. and Hikosaka, O. (2007). The role of the dorsal striatum in reward and decision-making. *The Journal of Neuroscience*, 27, 8161-8165.

Bianchin, M. & Angrilli, A. (2011). Decision Preceding Negativity in the Iowa Gambling Task: an ERP study. *Brain and Cognition*, 75, 273-80.

Blavatskyy, P.R. (2009). Preference reversals and probabilistic decisions. *Journal of Risk and Uncertainty*, 39, 237-250.

Bleichrodt, H. and Prades, J.L.P. (2009). New evidence of preference reversals in health utility measurements. *Health Economics*, 18, 713-726.

Botvinick, M.M. (2007). Conflict monitoring and decision making. Reconciling two perspectives on anterior cingulate function. *Cognitive, Affective and Behavioral Neuroscience*, 7, 356-366.

Botvinick, M.M., Cohen, J.D. and Carter, C.S. (2004). Conflict monitoring and anterior cingulate cortex: an update. *Trends in Cognitive Sciences*, 8, 539-546.

Breiter, H.C., Aharon, I., Kahneman, D., Dale, A. and Shizgal, P. (2001). Functional imaging of neural responses to expectancy and experience of monetary gains and losses. *Neuron*, 30, 619-639.

Butler, J.D. and Loomes, G.C. (2007). Imprecision as an account of the preference reversal phenomenon. *American Economic Review*, 97, 277-297.

Calder, A.J., Lawrence, A.D. and Young A.W. (2001). Neuropsychology of fear and loathing. *Nature Reviews Neuroscience*, 2, 352-363.

Chandrasekhar, P.V., Capra, C.M., Moore, S., Noussair, C. & Berns, G.S. (2008). Neurobiological regret and rejoice functions for aversive outcomes. *NeuroImage*, 39, 1472-1484.

Chang, L.J., Yarkoni, T., Win Khaw, M. & Sanfey, A.G. (2012). Decoding the role of the insula in human cognition: Functional parcellation and large-scale reverse inference. *Cerebral Cortex*. Advance online publication. doi:10.1093/cercor/bhs065.

Cisek, P. & Kalaska, J.F. (2005). Neural correlates of reaching decisions in dorsal premotor cortex: specification of multiple direction choices and final selection of action. *Neuron*, 45, 801-814.

Clark, L., Bechara, A., Damasio, H., Aitken, M.R.F., Sahakian, B.J. and Robbins, T.W. (2008). Differential effects of insular and ventromedial prefrontal cortex lesions on risky decision-making. *Brain*, 131, 1311-1322.

Cunningham, W.A., Kesek, A. and Mowrer, S.M. (2008). Distinct orbitofrontal regions encode stimulus and choice valuation. *Journal of Cognitive Neuroscience*, 21, 1956-1966.

Dehaene, S., Dehaene-Lambertz, G. and Cohen, L. (1998). Abstract representations of numbers in the animal and human brain. *Trends in Neuroscience*, 21, 355-361.

Dehaene, S., Molko, N., Cohen, L. and Wilson, A.J. (2004). Arithmetic and the brain. *Current Opinions in Neurobiology*, 14, 218-224.

Dehaene, S. (2009). Origins of mathematical intuitions: The case of arithmetic. *Annals of the New Year Acadamy Science*, 1156, 232-259.

Deppe, M., Schwindt, W., Krämer, J., Kugel, H. Plassmann, H., Kenning, P. and Ringelstein, E.B. (2005). Evidence for a neural correlate of a framing effect: Bias-specific activity in the ventromedial prefrontal cortex during credibility judgments. *Brain Research Bulletin*, 67, 413-421.

De Martino, B., Kumaran, D., Holt, B. and Dolan, R.J. (2009). The neurobiology of reference-dependent value computation. *The Journal of Neuroscience*, 29, 3833-3842.

De Martino, B., Kumaran, D., Seymour, B. and Dolan, R.J. (2006). Frames, biases, and rational decision-making in the human brain. *Science*, 313, 684-687.

De Visser, L., van der Knaap, L.J., van de Loo, A.J.A.E., van der Weerd, C.M.M., Ohl, F. and van den Bos, R. (2010). Trait anxiety affects decision-making differently in healthy men and women: Towards gender-specific endophenotypes of anxiety. *Neuropsychologia*, 48, 1598-1606.

Elliott, R., Agnew, Z. and Deakin JF. (2008). Medial orbitofrontal cortex codes relative rather than absolute value of financial rewards in humans. *European Journal of Neuroscience*, 27, 2213-2218.

Engelmann, J.B. and Tamir, D. (2009). Individual differences in risk preference predict neural responses during financial decision-making. *Brain Research*, 1290, 28-51.

Fishburn P.C. (1985). Nontransitive preference theory and the preference reversal phenomenon. *Rivista Internazionale di Science Economiche e Commerciali*, 32, 39-50.

Fitzgerald, T.H.B, Seymour, B. and Dolan, R.J. (2009). The role of human orbitofrontal cortex in value comparison for incommensurable objects. *Journal of Neuroscience*, 29, 8388-8395.

Goldstein, W. and Einhorn, H.J. (1987) Expression theory and the preference reversal phenomenon. *Psychological Review*, 94, 236-254.

Grether, DM. and Plott, C.R. Economic theory of choice and the preference reversal phenomenon. *Am Econ Rev*, 69, 623-638.

Guala, F. (2000). Artefacts in experimental economics: preference reversals and the Becker-DeGroot-Marschak mechanism. *Econ Philos*, 16, 47-75.

Haber, S.N. & Knutson, B. (2009). The reward circuit: Linking primate anatomy and human imaging. *Neuropsychopharmacology*, 35, 4-26.

Hausman, DM. (1991). On dogmatism in economics: The case of preference reversals. Journal of Socio-Economics, 20, 205-225.

Heilman, R.M., Crişan, L.G. Houser, D., Miclea, M. and Miu, A.C. (2010). Emotion regulation and decision making under risk and uncertainty. *Emotion*, 10, 257-265.

Holt, C.A. (1986). Preference reversals and the independence axiom. *American Economic Review*, 76, 508-515.

Hsee, C.K. (1998). Less is better: When low-value options are valued more highly than high-value options. *Journal of Behavioral Decision-Making*, 11, 107-121.

Jost, K., Khader, P.H., Burke, M., Bien, S. & Rössler, F. (2011). Frontal and parietal contributions to arithmetic fact retrieval: a parametric analysis of the problem-size effect. *Human Brain Mapping*, 32, 51-59.

Kable, J.W. and Glimcher, P.W. (2009). The neurobiology of decision: Consensus and controversy. *Neuron*, 63, 733-745.

Kahneman, D., Knetsch, J.L. and Thaler, R.H. (1990). Experimental tests of the endowment effect and the coarse theorem. *The Journal of Political Economy*, 98, 1325-1348.

Kahneman, D. and Tversky, A. (1979). Prospect theory: An analysis of decision under risk. *Econometrica*, 47, 263-292.

Kalenscher, T., Tobler, P.N., Huijbers, W., Daselaar, S.M. and Pennartz, C.M.A. (2010). Neural signatures of intransitive preferences. *Frontiers in Human Neuroscience*, 4, 1-14.

Karni, E. and Safra, Z. (1987). 'Preference reversals' and the observability of preferences by experimental methods. *Econometrica*, 55, 675-685.

Kim, S., Hwang, J., Seo, H. and Lee, D. (2009). Valuation of uncertain and delayed rewards in primate prefrontal cortex. *Neural Networks*, 22, 294-304.

Kringelbach, M.L. (2004). Food for thought: hedonic experience beyond homeostasis in the human brain. *Neuroscience*, 126, 807-819.

Lee, D. (2008). Game theory and neural basis of social decision making. *Nature Neuroscience*, 11, 404-409.

Li, X., Lu, Z.L., D'Argembeau, A., Ng, M. and Bechara, A. (2009). The Iowa Gambling Task in fMRI images. *Human Brain Mapping*, 31, 410-423.

Lichtenstein, S. and Slovic, P. (1971). Reversals of preferences between bids and choices in gambling decisions. *Journal of Experimental Psychology*, 89, 46-55.

Lichtenstein, S. and Slovic, P. (1973). Response-induced reversals of preference in gambling: An extended replication in Las Vegas. *Journal of Experimental Psychology*, 101, 16-20.

Lichtenstein, S. and Slovic, P. (2006). *The Construction of Preference*. Cambridge University Press, Cambridge.

Lindman H. (1971). Inconsistent preferences among gambles. *Journal of Experimental Psychology*, 89, 390-397.

Liu, X., Hairston, J., Schrier, M. and Fan, J. (2011). Common and distinct networks underlying reward valence and processing stages: A meta-analysis of functional neuroimaging studies. *Neuroscience and BioBehavioural Reviews*, 35, 1219-1236.

Loomes, G. (2009) Modeling choice and valuation in decision experiments. *Psychological Review*, 117, 3, 902-924.

Loomes, G. and Sugden, R. (1983). A rationale for preference reversal. *American Economic Review*, 73, 428-432.

MacDonalds, D.N, Huth, W.L. and Taube, P.L. (1992). Generalized expected utility analysis and preference reversals. *Journal of Economic Behavior and Organization*, 17, 115-130.

McCoy, A.N. and Platt, M.L. (2005[1]). Expectations and outcomes: decision-making in the primate brain. *Journal of Computational Physiology A: Sensory, Neural nad Behavioural Physiology*, 191, 201-211.

McCoy, A.N. and Platt, M.L. (2005[2]). Risk-sensitive neurons in macaque posterior cingulate cortex. *Nature Neuroscience*, 8, 1220-1227.

Menon, V. & Uddin, L.Q. (2010). Saliency, switching, attention and control: a network model of insula function. *Brain Structure and Function*, 214, 655-667.

Miller, E.K. and Cohen, J.D. (2001). An integrative theory of prefrontal cortex function. *Annual Reviews of Neuroscience*, 24, 167-202.

Miu, A.C., Heilman, R.M. and Houser, D. (2008). Anxiety impairs decision-making: Psychophysiological evidence from an Iowa gambling task. *Biological Psychology*, 77, 353-358.

Mohr, P.N.C., Biele, G. and Heekeren, H.R. (2010). Neural processing of risk. *The Journal of Neuroscience*, 30, 6613-6619.

Montague, P.R. and Berns, G.S. (2002). Neural economics and the biological substrates of valuation. *Neuron*, 36, 265-284.

Oliver, A. (2006). Further evidence of preference reversals: Choice, valuation and ranking over distributions of life expectancy. *Journal of Health Economics*, 25, 803-820.

Passingham, R.E., Bengtsson, S.L. & Lau, H.C. (2010). Medial frontal cortex: from self-generated action to reflection on one's own performance. *Trends in Cognitive Science*, 14, 16-21.

Pastor-Bernier, A. & Cisek, P. (2011). Neural correlates of biased competition in premotor cortex. *Journal of Neuroscience*, 31, 7083-7088.

Pesaran, B., Nelson, M.J. and Andersen, R.A. (2008). Free choice activates a decision circuit between frontal and parietal cortex. *Nature*, 453, 406-410.

Peters, J. and Büchel, C. (2009). Overlapping and distinct neural systems code for subjective value during intertemporal and risky decision making. *The Journal of Neuroscience*, 29, 15727-15734.

Platt, M.L. and Glimcher, P.W. (1999). Neural correlates of decision variables in parietal cortex. *Nature*, 400, 233-238.

Polezzi, D., Sartori, G., Rumiati, R., Vidotto, G. and Daum, I. (2010). Brain correlates of decision-making. *NeuroImage*, 49, 1886-1894.

Price, C.J. (2010). The anatomy of language: a review of 100 fMRI studies published in 2009. *Annals of the New York Academy of Sciences*, 1191, 62-88.

Quartz, S.R. (2009). Reason, emotion and decision-making: risk and reward computation with feeling. *Trends in Cognitive Sciences*, 13, 209-215.

Rangel, A., Camerer, C. and Montague, P.R. (2008). A framework for studying the neurobiology of value-based decision making. *Nature Reviews Neuroscience*, 9, 545-556.

Ridderinkof, K.R., Ullsperger, M., Crone, E.A. and Nieuwenhuis, S. (2004). The role of the medial frontal cortex in cognitive control. *Science*, 306, 443-447.

Riviera, S.M., Reiss, A.L., Eckert, M.A. and Menon, V. (2005). Developmental changes in mental arithmetic: Evidence for increased functional specialization in the left inferior parietal cortex. *Cerebral Cortex*, 15, 1779-1790.

Roiser, J.P., de Martino, B., Tan, G.C.Y, Kumaran, D., Seymour, B., Wood, N.W. and Dolan, R.J. (2009). A genetically mediated bias in decision making driven by failure of amygdala control. *Journal of Neuroscience*, 29, 5985-5991.

Sanfey, A.G., Rilling, J.K., Aronson, J.A., Nystrom, L.E. and Cohen, J.D. (2003). The neural basis of economic decision-making in the Ultimatum Game. *Science*, 300, 1755-1758.

Segal, U. (1988). Does the preference reversal phenomenon necessarily contradict the independence axiom? *American Economic Review*, 78, 233-236.

Seidl, C. (2002). Preference reversal. *Journal of Economic Surveys*, 16, 621-655.

Seitz, R.J., Franz, M. & Azari, N.P. (2009). Value judgments and self-control of action: The role of the medial frontal cortex. *Brain Research Reviews*, 60, 368-378.

Slovic, P. and Lichtenstein, S. (1968). Relative importance of probabilities and payoffs in risk taking. *Journal of Experimental Psychology*, 78, 1-18.

Smoski, M.J., Lynch, T.R., Rosenthal, M.Z., Cheavens, J.S., Chapman, A.L. and Krishnan, R.R. (2008). Decision-making and risk aversion among depressive adults. *Journal of Behavior Therapy and Experimental Psychiatry*, 39, 567-576.

Stanescu-Cosson, R., Pinel, P., van De Moortele, P.F., Le Bihan, D., Cohen, L. & Dehaene, S. (2000). Understanding dissociations in dyscalculia: a brain imaging study of the impact of number size on cerebral networks for exact and approximate calculation. *Brain*, 123, 2240-2255.

Talairach, J. & Tournoux, J. (1988). *Coplanar stereotactic atlas of the human brain*. Thieme Medical Publishers, New York.

Thaler, R.H. (1988). Anomalies: The winner's curse. *J Econ Perspect*, 2, 191-202.

Tom, S.M., Fox, C.R., Trepel, C. & Poldrack, R.A. (2007). The neural basis of loss aversion in decision-making under risk. *Science*, 315, 515-518.

Tversky, A., Slovic, P. and Kahneman, D. (1990). The causes of preference reversal. *American Economic Review*, 80, 204-217.

Vickery, T.J. and Jiang, Y.V. (2009). Inferior parietal lobule supports decision making under uncertainty in humans. *Cerebral Cortex*, 19, 916-925.

Vogt, B.A., Berger, G.R. and Derbyshire, S.W.G. (2003). Structural and functional dichotomy of human midcingulate cortex. *European Journal of Neuroscience*, 18, 3134-3144.

Vogt, B.A., Finch, D.M. & Olsen, C.R. (1992). Functional heterogeneity in cingulate cortex: The anterior executive and posterior evaluative regions. *Cerebral Cortex*, 2, 435-443.

Watson, K.K. (2008). Evolution, risk, and neural representation. *Annals of the New York Academy of Sciences*, 1128, 8-12.

Zheng, H., Wang, X.T. and Zhu, L. (2010). Framing effects: Behavioral dynamics and neural basis. *Neuropsychologia*, 48, 3198-3204.

Figure 1. Schematic of single Valuation task (Val-Rew) trial. Shown is an example of a valuation trial and a control trial. Following a valuation trial the participant indicated their valuation on a visual analogue scale which ranged from £1 to £200 in £10 intervals. So that the participant made a motor movement in the control trials, they were instructed to move the slider to £200.

Figure 2. Schematic of a Forced choice task (Choice-Rew) trial. A forced-choice and control trial are shown. In the forced-choice trial participants made a choice between two alternatives. So that the participants also made a motor response in the control trials they were instructed to press the button corresponding to the "alternative" that was underlined.

Figure 3. Mean valuations from the Val-Rew and Val-Loss (upper panels). True expected value is indicated by the dotted lines and mean subject valuations by the solid line. Error bars show 2 standard errors from the mean. The distribution of preference reversals and choices relative to valuations from the Choice-Rew and Choice-Loss are also shown (lower panel bar plots) plotted against difference in expected value between the P-bet and $-bet for each gamble pair. The area of the bar labelled "Other" includes instances where valuations of the two were equal.

Figure 4. Multislice overlay image of activity displayed on standard T1 MRI template showing activity the Val-Rew (red), Val-Loss (blue), Choice-Rew (green) and Choice-Loss (yellow) conditions. The lateral and medial frontal regions were consistently activated during the valuation of gamble (gamble minus control trial contrast). For forced choice conditions additional activity is seen in the posterior parietal cortices and anterior cingulate (threshold, $p<.001$, cluster threshold, $p<.05$).

Figure 5. Areas of increased activity revealed by the contrast of valuation vs. choice tasks (red regions) and choice tasks vs. the valuations tasks (blue regions) independent of gamble type (reward / loss) (threshold, $p<.001$, cluster threshold, $p<.05$).